

Reflections on the *Hyperolius nasutus* group (Anura, Hyperoliidae)

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Species delimitation, species characterization and nomenclature are confused and unsettled in the African *Hyperolius nasutus* group. A recent paper changing the nomenclature fundamentally, solely based on mating calls, is commented critically. The present paper claims that *H. lamottei* Laurent, 1958 should be maintained as a species separate from central African forms, that *H. viridis* Schiøtz, 1975 is not the same species as *H. viridis* sensu Channing et al. (2002), that the use of the name *H. acuticeps* Ahl, 1931 for the widespread savanna form is not so convincingly established that it justifies the dramatic change from the presently used name, *H. nasutus* Günther, 1865, and that the arguments for naming a central-western form *H. nasutus* rather than *H. adspersus* Peters, 1877 seem weak. Finally the name *H. benguellensis* (Bocage, 1893) seems synonymized on slender grounds. It is suggested that voice alone is not sufficient to characterize species in this group.

INTRODUCTION

The African *Hyperolius nasutus* group (Anura, Hyperoliidae) is very characteristic within the genus, consisting of small, slender, sharp-nosed frogs where both sexes are of the same size and where eggs are placed in water rather than above the water-line. In life, the frogs are translucent green, a colour which after preservation fades to white or light yellow.

The group consists of several species with a very similar morphology. A combination of morphological similarity, often very general original descriptions and, in several cases, loss of type specimens has contributed substantially to the present state of nomenclatural uncertainty. The problem is further compounded in that some characters, like call differences, ear anatomy, colour pattern, shape of snout and webbing suggest different species delimitation. Several recent papers have contributed to our knowledge, without reducing our confusion. Below, the proposed species delimitation and nomenclatural changes are commented upon.

HISTORY

Fifteen names have been used for members of the group of which many have at one time or another been synonymized. A list of these names is given in AMIET (2005)

POYNTON & BROADLEY (1987) recognized three species in the southern African savanna, *H. viridis* Schiøtz, 1975, *H. nasutus* Günther, 1865 and *H. benguellensis* (Bocage, 1893), the latter being their name for SCHIÖTZ' (1975) *H. granulatus* (Boulenger, 1901). SCHIÖTZ (1999) concluded that the species distinction between *H. nasutus* and *H. benguellensis* based on morphology and pattern of preserved specimens seems too ill-defined and inconstant to necessitate the recognition of two species. However, the distinction between these two species, *H. nasutus* and *H. benguellensis*, was established by WILSON in an unpublished paper, based on anatomical differences of the tympanic apparatus.

SCHIÖTZ & DAELE (2003) collected two species in Hillwood, north-western Zambia, sympatric but not syntopic and clearly distinguishable by their voice. They used the names *H. nasutus* and *H. benguellensis*.

AMIET (2005) in a study of the complex occurring in Cameroun, using voice, morphology and habitat preference, reached the conclusion that there are two species in that country. Amiet chose the name *H. igbettensis* Schiøtz, 1963 for the northern, savanna-living form to indicate it being conspecific with material from Nigeria to central Côte d'Ivoire, but he did not reject it being conspecific with one of the forms from the savanna further east and south in Africa. The other Camerounese species is found in clearings in the forest ("parasyllivicolous" according to Amiet's terminology) in southern Cameroun and was given the name *H. adpersus* Peters, 1877 (type locality: Cabinda, Angola). Amiet's meticulous study revealed subtle differences in morphology between the two species in addition to significant differences in habitat preference and voice.

THE NOMENCLATURE OF CHANNING ET AL. (2002)

A profound revision of the nomenclature traditionally used in the group was published by CHANNING et al (2002). Based on recordings of mating calls throughout Africa, they divided the complex in three species, *H. acuticeps* Ahl, 1931, *H. viridis* Schiøtz, 1975 and *H. nasutus* Günther, 1865, none of the three names being congruent with previous uses. Their distinction is based solely on the voices, disregarding morphological similarities and differences. They divided their material based on 3 call types ("A, B and C"). The most widespread savanna form with a call type A, in all recent literature termed *H. nasutus*, was given the name *H. acuticeps*. Instead the name *nasutus* was allocated to what I believe is an assemblage of species consisting of, or including, *H. lamotter* Laurent, 1958 and *H. adpersus* Peters, 1877 sensu AMIET (2005). The name *H. viridis* was used for what I believe is POYNTON & BROADLEY'S (1987) and Wilson's *H. benguellensis* (Bocage, 1893), not *H. viridis* Schiøtz, 1975. The name *H. lamotter* was wrongly attributed to the species *nasutus* and the name *H. igbettensis* was (p. 96) placed as a synonym of *H. nasutus* in error (the call is of type A, not C, as stated on p. 96, correct in fig.3). These forms are discussed below.

CHANNING et al (2002) proposed formal changes in nomenclature and gave detailed lists of synonyms. Several of these nomenclatural allocations can in my opinion be questioned since the only species character they use, the voice, is for obvious reasons only preserved for type material in extraordinary cases. Instead they use the principle of parsimony, which in my

opinion is fraught with danger in a group with several sympatric species of similar morphology. Perhaps the principle of least disturbance should rather be used.

I have only encountered call C in the samples from Hillwood (Zambia) termed *H. nasutus* in SCHIOTZ & DAELLE (2003). My single confirmed sample of the voice of *H. benguelensis* from Hillwood is call type B (SCHIOTZ & DAELLE, 2003, fig. 2), all my remainder calls from Africa are of type A 2.

***Hyperolius lamottei* Laurent, 1958**

H. lamottei Laurent, 1958 (type locality between Zougouépo and Sérengbara, Guinca) is included in CHANNING et al.'s (2002) species *H. nasutus* based on the voice which, according to them, is of type C. The sonogram (SCHIOTZ, 1967 fig. 118-119; 1999 fig. 170), however, shows a voice of *lamottei* quite dissimilar in structure to their type C, with a large number of harmonics of almost equal energy which gives the voice a very characteristic acoustical quality, different from that of their call type C. A closer analysis of a call type C, namely AMÉRY's (2005) recording of his *H. adpersus* from Olembé (*H. nasutus* sensu CHANNING et al., 2002) does not disclose such a structure with many harmonics. The frequency intensity maximum of the voice from Olembé is 4.9 kHz, of *H. lamottei* 3.9 kHz (analysis kindly realized by Dr. T. Dabelsteen, Zoological Institute, Copenhagen University). My recorded voices of *H. lamottei* from both ends of the range, almost 1000 km apart (Freetown, Sierra Leone and Lamto, Côte d'Ivoire) are identical in structure.

The argument for *H. lamottei* and CHANNING et al.'s (2002: 97) *nasutus* being conspecific, rests partly on a citation from SCHIOTZ (1999), but is based on a misreading, as my comparison was with what I then termed *H. nasutus* (largely, Channing et al.'s *H. acuticeps*). The colour range of *H. lamottei* is actually quite distinct from that of the other members of the group, the alleged distribution of Channing et al.'s *H. nasutus* is strangely disjunctive if *H. lamottei* is included, and CHANNING et al.'s (2002: 97) information that this form in Côte d'Ivoire is a forest form is incorrect, as it is strictly a savanna species. RÖDHL & ERNST (2003) has therefore correctly re-established *H. lamottei* as a distinct species.

***Hyperolius viridis* Schiötz, 1975**

CHANNING et al.'s (2002) use of the name *H. viridis* Schiötz, 1975 (type locality 30 miles south-west of Mbeya, Tanzania) as one of their three recognized species may be based on a misidentification of their collected material. *H. viridis* is a species quite different in morphology from members of the *nasutus* group, in fact so different that it was originally (SCHIOTZ, 1975, 1999) not even considered belonging to the *nasutus* group and was not compared to that group, but only to *H. pusillus*. CHANNING et al.'s (2002) use of the name seems to be based not on an examination of the type material in the Zoological Museum of Copenhagen, but solely on their "voucher material" collected in the Sumbawanga district, close to the type locality of *H. viridis*. Such identification by locality should, however, be regarded with reservation since both *H. nasutus* and *H. benguelensis* (names sensu POYNIS & BROADBENT, 1987) occur in this general area in addition to *H. viridis*. Therefore, since they have been unable to distinguish

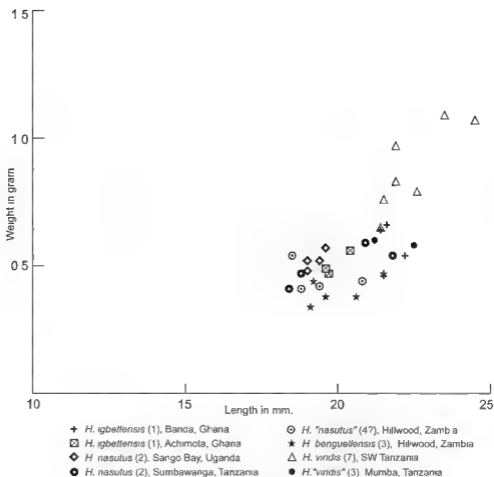


Fig 1. Snout-vent length in millimetres versus weight in gram of preserved animals. Numbers in brackets refer to the species numbers in table I

between living and preserved voucher specimens of *H. viridis* and *H. acuticeps* collected side-by-side at Mumba" (CHANNING et al., 2002: 92), it seems most likely that they have collected the two very similar (sometimes morphologically indistinguishable) species *H. nasutus* and *H. benguelensis*, not the diverging *H. viridis*.

A major difference between *H. viridis* and the *H. nasutus* group is that the latter consist of slender frogs, *H. viridis* being much more massive. This is difficult to express through measurements of body dimensions, instead I have attempted to express this feature through the weight of preserved animals (fig 1). There are several sources of error in such measurements, but I believe it is defensible when used for a comparison between taxa. All specimens in figure 1 are males collected when calling, all were kept 10-12 hours in a plastic bag before

preservation so they have no stomach contents, and they have been preserved in 70% alcohol without injection. The weight of the attached museum numbers is deducted. *H. viridis* is clearly separate from the *H. nasutus* group, being only slightly larger but much heavier (fig. 1). This is not in agreement with CHANNING et al.'s (2002) description of their *H. viridis*. No other taxa are distinctive in these features.

Alan Channing kindly sent me two males of "*H. viridis* sensu CHANNING et al., 2002" from Mumba, south-western Tanzania. By being slender and sharp-nosed (fig. 1-2), they differ clearly from the massive *H. viridis* Schiötz, 1975. Furthermore, one of the specimens has very conspicuous paravertebral stripes in addition to the dorsolateral stripes, a distinguishing character for some, but not all, specimens of *H. benguellensis*. My conclusion is that the two specimens from Mumba is the same species as that called *H. benguellensis* by POYNTON & BROADLEY (1987) and by SCHIÖTZ & DAELE (2003).

My recorded calls of *H. viridis* (SCHIÖTZ, 1975, 1999, and unpublished calls from north of Mbeya) are of type A (A2 in Channing et al.'s terminology), whereas the call of *H. viridis* sensu CHANNING et al. is of type B (see CHANNING et al., 2002: fig. 1, compared with SCHIÖTZ, 1975: fig. 111, 1999: fig. 396). Here it is significant that my calls of *H. benguellensis* from Hillwood (SCHIÖTZ & DAELE, 2003 fig. 2) are of type B and thus are in agreement with what CHANNING et al. (2002) term *H. viridis* with an alleged call B, but different from that of my *H. viridis*.

Therefore, based on voice and morphology, I believe that *H. viridis* sensu CHANNING et al. (2002) is the same as *H. benguellensis* sensu POYNTON & BROADLEY (1987) and SCHIÖTZ & DAELE (2003), in which case the distribution of this species is much wider than that given by CHANNING et al. (2002) for their *H. viridis*, namely from south-western Uganda to Zimbabwe, Botswana, Caprivi Strip, Angola and southern République Démocratique du Congo, in many places sympatric with *H. nasutus* sensu POYNTON & BROADLEY (1987) and in a limited area sympatric with *H. viridis*.

One of the two records of CHANNING et al. (2002) for *H. viridis* is Hillwood (north-eastern Zambia), where the frogs, as in Mumba, were collected together with their *H. acuticeps* (see below, "the Hillwood mystery").

Hyperolius nasutus Günther, 1865

The name *H. nasutus* Günther, 1865 (type locality, Duque de Braganca, Angola) has for the last 140 years been used for the most widespread and abundant savanicolous form. This name is rejected for this widespread form by CHANNING et al. (2002) and the name *H. nasutus* restricted to a western species. Concerning *H. nasutus* sensu Channing et al., the long list of synonyms (and even the name *nasutus*) should be critically scrutinized since four out of the six synonyms, including the name *H. nasutus*, stand there "by parsimony" based on the assumption, without further proof, that *H. nasutus* is a species confined to western central Africa and that other species, for instance the species called *H. benguellensis*, are absent in the area. The only argument in several cases seems to be the "vicinity" to other records with or without known voices: for instance *H. benguellensis* was treated as a synonym of *H. nasutus*, the argument being that it was "collected 800 km south of the type locality for *H. nasutus* and we

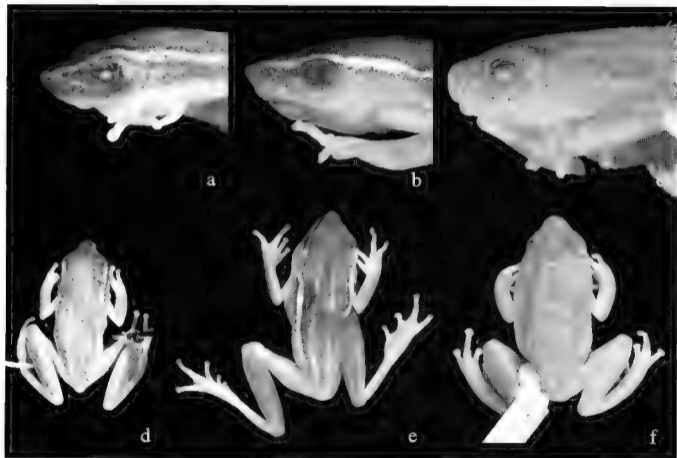


Fig. 2. Lateral and dorsal views of specimens of *Hesperolus* (a, d) *H. benguelensis* sensu Sc HIOTZ & DALE (2003), ZMUC R 076743, from Hihwood, Zambia (b, e) *H. "vulvix"* sensu CHANNING et al. (2002), ZMUC R 771392 (ex AC 2124), Mumba, Tanzania, Moyer leg., (c, f) *H. vulvix* Schotz 1975, ZML C R 099491 holotype, south-western Mbeya, Tanzania

Table 1. – Informal working list of presumed existing species in the *Hyperolius nasutus* group, and of *H. viridis* and *H. lamottei*. No formal nomenclatorial proposals intended. Names in bold are those used by CHANNING & al. (2002). References to uses of names: A: AMIET (2005); C: CHANNING et al. (2002); L: LAURENT (1943); P&B, POYNTON & BROADLEY (1987); S75, SCHIÖTZ (1975); S99, SCHIÖTZ (1977); S&D, SCHIÖTZ & DAELLI (2003); W: WILSON (unpub. sheet), n. a., not applicable.

Species number	Names used	Call	Distribution	Remarks
1	<i>nasutus</i> : S99 (part) <i>acuticeps</i> : C <i>benguelensis</i> : A	A2	Northern Cameroon to central Côte d'Ivoire	Probably conspecific with species 2
2	<i>nasutus</i> (part): P&B, S99, W <i>acuticeps</i> : C	A2	Eastern southern part of Africa	Probably conspecific with species 1
3	<i>gramulatus</i> : S75 <i>benguellensis</i> : P&B (part), W, S&D <i>viridis</i> : C	B	South-eastern Uganda to Zimbabwe to northern Botswana, Caprivi, Angola	Some specimens paravertebral lines; inner ear reduced; well pigmented, pointed snout
4	<i>nasutus</i> : C (part), S&D (?) <i>adpersus</i> : A	C	Southern Cameroon, possibly to coastal Angola, north-western Zambia, Caprivi (?), Botswana (?)	The only parasyticolous in complex, distinct voice
5	<i>nasutus</i> : L	?	Republique Democratique du Congo	Very sharp snout, status uncertain, possibly conspecific with species 1
6	<i>lamottei</i> : S99 <i>nasutus</i> : C	n. a.	Western West Africa	Distinct call and colour pattern: western vicariant of species 1
7	<i>viridis</i> : S75, P&B, S99	(A2)	South-western Tanzania, eastern Zambia	Morphologically distinct from the <i>nasutus</i> group

assign it to this species" (CHANNING et al., 2002: 96). Wilson has established the occurrence of what she calls *H. benguellensis* from Huila, Angola, just south-east of the type locality of *H. benguellensis*.

The widespread savanna form is called by CHANNING et al. (2002) *H. acuticeps* Ahl, 1931 instead of *H. nasutus* Günther, 1865. The somewhat strange argument is that the alleged call type of *H. acuticeps* (type A) is unknown from western Angola, the type locality of *H. nasutus*. The argument may not be entirely convincing since no voices of any species of the *Hyperolius nasutus* group have been recorded from Angola! CHANNING et al. (2002) used instead the species name *nasutus* for a form with a call type C and a distribution on "the west coast of Africa – and adjacent interior". The validity of their argument (and also their inclusion of *H. benguellensis* in the synonymy of *H. nasutus*) must hinge upon only one species of the *H. nasutus* group being present in Angola, which has not been demonstrated and seems unlikely. Although no recent collections have been made in Angola, it would seem reasonable to expect two savaniculous species there (sp. 2 and 3 according to table 1) and one parasyticolous (sp. 4), meaning that drastic changes in nomenclature based on "vicinity" or "parsimony", and implicitly based on an assumption that only one species is present, should be treated with some reservation.

Whereas the call of the holotype of *H. nasutus* obviously cannot be known, at least part of Channing et al.'s records of *H. nasutus* are referable to what AMIET (2005) termed *H. adpersus* (see below).

My remark in SCHIÖTZ & DAELLI (2003) that our *H. nasutus* from Hillwood had a voice "similar to the voice elsewhere in the range" is incorrect. Our sample had a call type C.

Hyperolius adspersus Peters, 1877

H. adspersus Peters, 1877 (type locality: Chinchoxo, Angola), the only parasympatric species in the complex, is, according to AMIET (2005), distributed from the southern (forested) half of Cameroun to coastal Gabon, south-western Republic of Congo (reported by LARGEN & DOWSETT-LEMAIRE, 1991, as *H. aff. nasutus*), lower République Démocratique du Congo and Cabinda (type locality), and probably coastal Angola down to 12°S. AMIET's (2005) *H. adspersus* is thus largely CHANNING et al.'s (2002) *H. nasutus* (excluding *H. lamottei*).

The possibility that SCHIÖTZ & DAELE's (2002) frogs with call type C from north-western Zambia, which they referred to *H. nasutus*, are in fact Amiet's *H. adspersus*, cannot be excluded. Amiet has kindly examined a sample of our *H. nasutus* from north-western Zambia (AMIET, 2005: 303), and reached the conclusion that they are very similar in voice and body dimensions to his *H. adspersus*, but differ in being somewhat smaller – not a good species character in this group – and having a shorter snout. Our locality for this species in north-western Zambia could be regarded as a locality for a parasympatric fauna.

If *H. nasutus* sensu SCHIÖTZ & DAELE (2002) from north-western Zambia is the same species as *H. adspersus* sensu AMIET (2005), it does expand the distribution considerably, but not unreasonably for a parasympatric species. Whether CHANNING et al.'s (2002) record of their *H. nasutus* from the Caprivi Strip and Okavango is the same ought to be investigated.

Hyperolius acuticeps Ahl, 1931

CHANNING et al. (2002) used the name *H. acuticeps* Ahl, 1931 (type locality: Konde-Nika, Tanzania) "since it appears most parsimonious", for what has hitherto been called *H. nasutus*, based on the type locality in an area where only call type A has been recorded but from where few recordings of members of the group are available. This is a bold move to change a name having been in common use for 140 years.

The many records in the literature of *H. nasutus* from Ethiopia and eastern and southern Africa were not specifically treated by CHANNING et al. (2002), but it can be implied by their maps that they should be referred to *H. acuticeps*.

Hyperolius benguellensis (Bocage, 1893)

Hyperolius benguellensis (Bocage, 1893) (type locality: Cahata, Benguella, Angola) remains an enigmatic species. If CHANNING et al.'s (2002) *H. nasutus* is the same as AMIET's (2005) parasympatric *H. adspersus*, and if *H. viridis*, both in Schiötz' and in Channing's sense, has a very restricted distribution ("highlands linking the eastern and western Rift valleys in northern Zambia and southern Tanzania", according to CHANNING et al., 2002), there remains a question not addressed by CHANNING et al. (2002): what is the status and correct name for what has reasonably convincingly been established as a distinct species, called *H. benguellensis* by POYNTON & BROADLEY (1987) and WILSON (unpublished), with a wide distribution (maps in POYNTON & BROADLEY, 1991, and in WILSON, unpublished)?

POYNTON & BROADLEY's (1987) study left much doubt about the distinction between *H. benguelensis* and their *H. nasutus*. SCHIÖTZ (1999) was therefore reluctant to recognize the two species based on the rather inconstant distinguishing characters. WILSON (unpublished) seemed to point at an objective difference between them. SCHIÖTZ & DAELF (2003) were able to distinguish clearly between two species at Hillwood, but since their *H. nasutus* might be AMIET's (2005) *H. adpersus*, we still lack an authoritative comparison between the two widespread savanna species, *H. nasutus* and *H. benguelensis* sensu Poynton & Broadley. SCHIÖTZ & DAELF (2003) separated their two species from Hillwood (sympatric but apparently not syntopic) based on the voice, and showed that the "benguelensis character", light paravertebral stripes in addition to the dorsolateral stripes, is unsuited as a diagnostic character since it is only present in about 15% of our material of males with *benguelensis* call. The voice, call B, and Wilson's ear character may be diagnostic for *H. benguelensis*.

CHANNING et al (2002) included *H. benguelensis* (type locality: Cahata, Benguella, Angola) in the synonymy of *H. nasutus* (type locality: Duque de Braganca, Angola) purely based on "proximity" (800 km⁴) of the type localities, but they did not discuss the status of the large quantity of material of *H. benguelensis* from Botswana, Zambia, Malawi and Zimbabwe treated by POYNTON & BROADLEY (1987) and by WILSON (unpublished), the latter also including material from République Démocratique du Congo, Uganda and Angola. WILSON (unpublished) had unfortunately examined very few samples of the two species from East Africa. One of the samples of *H. benguelensis* examined by Wilson is from Huila (Angola), quite close to the type locality of that species, which may point at *H. benguelensis* being the correct name for the species (by parsimony!).

SCHIÖTZ & DAELF's (2003) record of the voice of *H. benguelensis* (call type B) seems to be the only record where the call has definitely been correlated with pattern, webbing and with Wilson's own examination of the inner ear in our sample (Wilson, personal communication).

My photo of a typical *H. benguelensis* with paravertebral stripes (SCHIÖTZ, 1975, fig. 98, 1999: fig. 164) was referred to *H. acuticeps* by CHANNING et al (2002, 96)

Hyperolius nasicus Laurent, 1943

H. nasutus Laurent 1943 (type locality: Kasiki, Marungu, République Démocratique du Congo) has not been mentioned in the literature recently. In the Royal Museum of Central Africa, Tervuren I found a few samples from République Démocratique du Congo identified by Laurent as that species (or *H. nasutus nasicus*). The type material from north-eastern Congo has a very pointed, shark-like snout. The four half-grown paratypes of *H. nasutus* from the type locality have retained conspicuous white dorsolateral lines after preservation, unusual for the *H. nasutus* group since the light stripes normally tend to disappear when the green ground colour vanishes after preservation. The male holotype (snout-vent length 23.4 mm) of *H. nasutus* is unstriped. I feel that *H. nasutus* should be compared to *H. benguelensis* which also has a pointed snout and so much pigmentation that the light dorsolateral stripes often are visible after preservation. *H. nasutus* is further discussed in SCHIÖTZ (2006).

THE HILLWOOD MYSTERY

Hillwood in Mwinilunga district (north-western Zambia) is a well-investigated locality. It has provided material of two species treated by SCHIÖTZ & DAELLE (2003) as *H. nasutus* and *H. benguellensis*, and by CHANNING et al. (2002) as *H. acuticeps* and *H. viridis*. The actual collecting localities seem to be the same: when Schiøtz and Daele visited Hillwood in 1999, we were shown the localities where Channing and Drewes had collected their material a few years previously ("Pauls fishpond" and a small inundated meadow on the way to the guest-huts).

A direct comparison between our observations and those of CHANNING et al. (2002) is complicated by Schiøtz and Daele finding call types B ("*benguellensis*") and C ("*nasutus*"), whereas Channing and Drewes in allegedly the same two localities found call types B ("*viridis*") and A ("*acuticeps*"). CHANNING et al.'s (2002) call types A and B may, to judge from their descriptions and published sonograms, be easy to confuse but type C seems quite unmistakable.

CONCLUSION

Voice alone may not be sufficient to characterize species in the *Hyperolius nasutus* group, and voice in combination with the principle of parsimony is insufficient to allocate names to species, considering several cases of sympatric occurrence and considering that the voice of type material is only known in two cases (species 1 and 7, table 1).

There seem to be between five and seven species in the group (table 1)

Species 6 and 7 seem well defined and their names (*H. lamottei* and *H. viridis*) established.

Species 4 is well-defined by non-morphological characters (voice and habitat). The name *H. adspersus* is not certain.

Species 1 and 2 may be conspecific, their nomenclature is unsettled.

Species 3 and 5 are badly defined, especially in relation to species 2, and incompletely known.

Although members of the *Hyperolius nasutus* group are abundant and easy to collect, we lack material from many areas, for instance the savanna between Cameroun and Ethiopia and from Angola and southern République Démocratique du Congo, and we lack recordings from even more areas. In this connection it should be mentioned that all the authors' recordings are placed at the Library of Natural Sounds, Cornell University, and at the Zoological Museum, Copenhagen.

Nomenclatural changes in the *Hyperolius nasutus* group should be based on a broad spectrum of morphological and non-morphological characters, including the voice, and on studies of DNA.

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